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PERCEPTION OF CERTAIN MECHANICAL QUANTITIES INHERENT TO THE ANIMAL ORGANISM

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PERCEPTION OF CERTAIN MECHANICAL QUANTITIES INHERENT TO THE ANIMAL ORGANISM */11

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The properties of an elementary model of the otolithic portion of the vestibular apparatus, explaining a number of functions of this important organ, are examined. The principles of measuring a number of mechanical parameters necessary for control and coordination of movements are hypothesized on the basis of analyzing the experimental materials and properties of the model, in analogy with data-processing systems for conversion of analog to digital data. Orientation in space, upon deflection of the head from the vertical, and under acceleration, is discussed on the basis of function of the receptor-neuron circuits of the otolithic apparatus. AUTHOR

During their vital activity, animals constantly change the position of their bodies in space. In addition to other organs, the vestibular apparatus plays a major role in the control of the spatial positioning of the body and organization of the coordination of movements. One of its functions should evidently be the "measurement" of a number of mechanical parameters or factors, required for generating, in the central nervous system of the animal, certain control signals that are then fed to the input of the "actuating mechanisms" (organs of motion).

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* Numbers in the margin indicate pagination in the original foreign text.

A study of the principles of the "measurement" of mechanical parameters inherent to animals, i.e., the principles of the conversion of these parameters by receptors into electrical signals and the principles of information "processing" in the central nervous system can be of definite interest for specialists engaged in the area of developing data-processing systems.

Using, as an example, the properties of an elementary model and functions of the otolithic portion of the vestibular apparatus, we will examine below the problem of the methods of the conversion, by this organ, of certain mechanical quantities into electrical ones.

1. Model of the Otolithic Portion of the Vestibular Apparatus

An important part of the spatial orientation analysor in higher animals is the vestibular apparatus which can be schematically represented as consisting of receptors receiving external stimuli and of neurons which connect the receptors with various formations of the nervous system.

The receptor part consists of the semicircular canals reacting primarily to angular accelerations and the otolithic apparatus perceiving linear movements of the head and body in space.

Whereas the mechanism of reception in the semicircular canals has been quite exhaustively explained, the concepts of the activity of the otolithic /12 apparatus are still rather disputable. It has been suggested that reception in the otolithic apparatus is accomplished by shifts of the gelatinous otolith membrane which is studded with crystals of lime (the otoliths) and with sensitive hair cells which penetrate the membrane for some distance.

To elucidate certain characteristics of the function of the otolithic apparatus on exposure of an animal to mechanical forces, we developed an elementary model of this important organ (Bibl.1, 2).

Figure 1 shows a structural diagram of the model, with the following basic properties:

a) The receptors of the otolithic portion of the vestibular apparatus (both the saccule and the utricle) represent generator transducers that convert

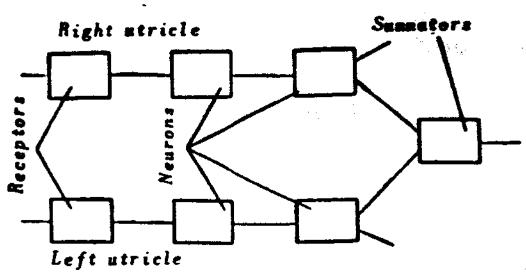

Fig.1 Block Diagram of the Elementary Model of the Otolithic Portion of the Vestibular Apparatus

the angle of deflection of the head of the animal from the vertical into frequency of electric pulses with a certain proportionality factor;

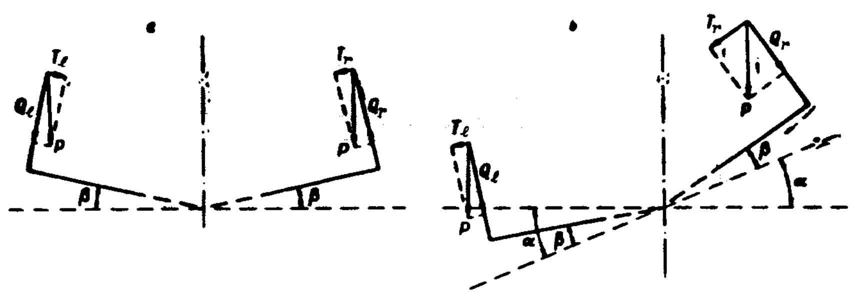

Fig.2 Function of the "Summator" of the Utricle in Statics
a - Vertical position of head; b - Inclination of head to the left through an angle α.

b) The receptor reacts to an inclination of the head relative to the vertical, as a consequence of the change in the magnitude of the component forces of the weight of the otoliths directed along and across the hairs of the receptor cells (Fig.2);

c) The otolithic apparatus consists of numerous circuits of receptor-neurons (R-Ns) having various dynamic properties;

d) The vestibular apparatus contains a "summator" which compares the frequency of the pulses arriving from the left and right utricles and from the saccule.

2. Principles of Conversion of Mechanical Parameters into Electrical Parameters Characteristic of the Otolithic Portion of the Vestibular Apparatus

As a result of studying the properties of the elementary model of the vestibular apparatus, hypotheses were formulated concerning the principle of "measuring" mechanical parameters characteristic of the otolithic portion of the vestibular apparatus. We assume these hypotheses to be confirmed if the /13 processes in the model correspond to the function of the real vestibular apparatus.

a) "Measurement" of the Magnitude and Direction of Deflection of the Head from the Vertical

The frequency of the pulses f_1 at the output of the R-Ns circuit of the right utricle (see Fig.2) representing the force directed along the hair cell is determined by the dependence

$$f_1 = k_1 P \cos(\alpha + \beta), \qquad (1)$$

where

P = force of the weight of the otolith;

k_1 = coefficient of sensitivity of the receptor along the hair cell;

α = angle of inclination of the head (in a frontal plane) relative to the horizontal;

β = angle of inclination of the plane of the utricle relative to the horizontal.

For a similar circuit of the left utricle, the pulse frequency corresponds to the expression

$$f_2 = k_2 P \cos(\alpha - \beta). \tag{2}$$

The output of the "summator", if we assume that $k_1 = k_2$, can be represented by

$$\Delta f = 2kP \sin\alpha \sin\beta. \tag{3}$$

It can be demonstrated that for the "channel" reacting to the force T (see Fig.2) directed across the hair cell, the output of the "summator" will have the form

$$\Delta f = 2kP \sin\alpha \cos\beta. \tag{4}$$

On the basis of analyzing these dependencies we can conclude that:

The frequency of the pulses at the output of the "summator" depends on the angle of inclination of the head relative to the longitudinal axis of the body.

Depending on the direction of inclination of the head, the signs of the summed quantities change with respect to the "channel" reacting to the force directed across the hair cell.

The presence of the angle β at inclination of the head, leads to a difference between signals arriving at the input of the "summator" from the left and right utricles with respect to the "channel" reacting to a force directed along the hair cell.

b) "Measurement" of the Magnitude and Direction of Linear Accelerations During Movements of the Animal

"Measurement" of the magnitude and sign of acceleration in a vertical plane was accomplished by a system which includes the receptors of the saccule and a "summator" which compares the signals arriving from the receptors of the anterior and posterior parts of the saccule.

Figure 3 shows a diagram of the relative position of the receptors of the anterior and posterior parts of the saccule in its sagittal plane (vertical plane perpendicular to the frontal).

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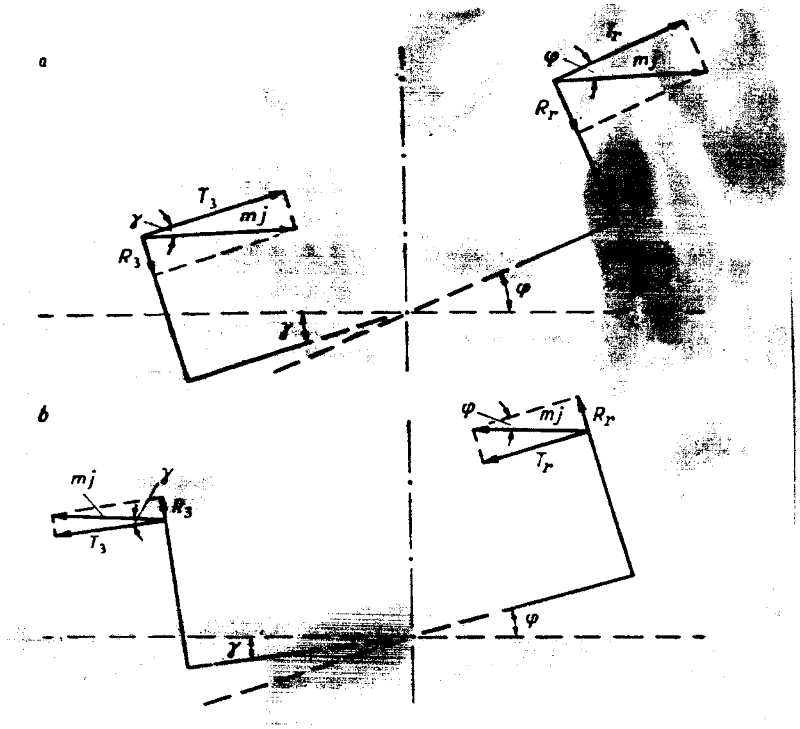

Fig.3 Diagram of Arrangement of the Saccule Receptors in a Sagittal Plane

The output of the "summator" when the acceleration j is directed "forward" (see Fig.3a) will be determined (provided we consider that one otolith is connected with each hair cell) by the following relationships:

With respect to the channel reacting to a force directed across the hair cells,

$$\Delta f^* = mjk_1^*(\cos\varphi - \cos\gamma), \tag{5}$$

and along the hair cell,

$$\Delta f^* = mjk_2^*(\sin\varphi - \sin\gamma), \tag{6}$$

where

φ = angle of elevation of the anterior part of the saccule, with respect to the horizontal;

γ = angle of inclination of the posterior part of the saccule, with respect to the horizontal;

m = mass of otolith.

When the acceleration is "backward" (see Fig.3b), the components of the output will be determined as

$$\Delta f^* = mk_1^* j(\cos\gamma - \cos\varphi), \tag{7}$$

$$\Delta f^* = mk_2^* j(\sin\gamma - \sin\varphi). \tag{8}$$

On the basis of analyzing these relationships we can conclude:

The components of the output of the "summator" are a linear function of the measured acceleration.

On change in sign of the acceleration ("backward" instead of "forward"), the signs of both components of the output of the "summator" also change. /15

If the equality $\varphi = \gamma$ were to exist in the model under consideration, then the output of the "summator" would always be equal to zero.

c) "Measurement" of the Magnitude and Direction of the Effect of Centrifugal Forces

Let us examine the functions performed by the "summator" during the circular flight of a bird. In this case (Fig.4), different forces will act upon the right and left otolithic apparatus. If a left turn is performed, the centrifugal force N_r, acting on the right otolith, can be represented by the relation

$$N_r = (r + 0.5l\cos\alpha)\,\omega^2, \tag{9}$$

where

r = radius of turn;

ℓ = distance between right and left otolithic apparatus;

ω = angular velocity of bird in turning.

The left otolith will be subject to the centrifugal force

$$N_l = (r - 0.5l\cos\alpha)\,\omega^2. \tag{10}$$

Since the pulse frequency in the receptors is proportional to the force acting on the receptor, the output of the "summator" in which both frequencies are compared, can be represented by

$$\Delta f = kl\omega^2 \cos\alpha. \tag{11}$$

This dependence [eq.(11)] is able to explain certain functions and principles of action of the mechanisms controlling the flight organs of birds. If the control system is tuned to a certain signal Δf_{opt}, which corresponds to turning without skidding, then for performing this maneuver with a greater angular velocity so as to maintain the same value of the output, the angle of inclination relative to the horizontal must be increased. This is precisely what takes place when both birds and man-made flying vehicles perform a turn.

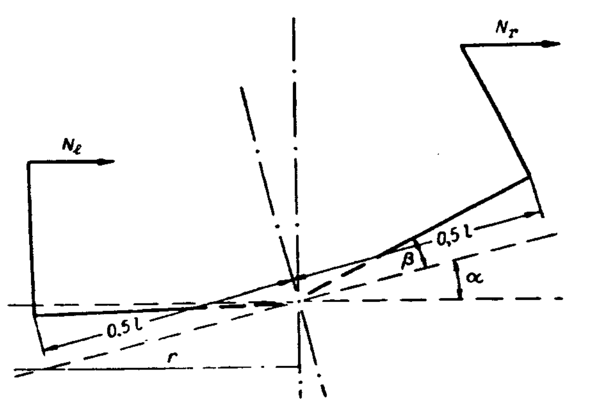

Fig.4 Function of the "Summator" of the Utricle in Dynamics

It is of interest to note that the proposed operating principle of the "summator" yields an explanation for the character of motion of animals and birds, in which the otolithic apparatus of one side has been extirpated.

Actually, when performing a left turn, the frequency of the pulses in the fibers of the right vestibular nerve, arriving at the input of the "summator", exceeds the pulse frequency in the left vestibular nerve, which changes the flight-control organs to a mode corresponding to a left turn. If the left /16 otolithic apparatus is removed, the sign of the output of the "summator" is retained, i.e., the flight-control organs in horizontal flight will be immediately brought into a left-turn mode.

Since the left otolithic apparatus is removed and the pulses from this apparatus will not arrive at the input of the "summator", the output of the "summator" will exceed the norm. If, on performing a turn, the system controlling the flight organs of the birds is tuned to a certain optimal value of the output of the "summator", then, as follows from eq.(11), the bird with the extirpated left otolithic apparatus should tend toward a maximal increase in the angle α, up to 90°.

These phenomena (Bibl.3) actually take place, which probably indicates that our hypotheses are correct.

d) "Measurement" of the Magnitude and Sign of Acceleration during Periodic Mechanical Vibrations

An investigation of the impulse activity of the neurons of the vestibular nuclei, on subjecting the animal to periodic oscillations, showed that

a) the pulse frequency at a fixed vibration period is proportional to the pulse amplitude;

b) there are R-Ns circuits that increase in activity when the animal moves "up" and decrease in activity when the animal moves "down", at diametrically opposite characteristics.

The peculiarities of the characteristics of the R-Ns circuits are explained by the dynamic properties of these circuits and the parameters of the mechanical vibrations.

Actually, if the animal is subjected to harmonic mechanical vibrations

(12)

(here h_0 is the vibration amplitude and ω is the vibration frequency), then the acceleration j suffered by the organism is determined – as is known – by the dependence

$$j=-h_0\,\omega^2 \sin \omega t. \tag{13}$$

Since the receptors of the vestibular apparatus generate a pulse frequency proportional to the G-force, we will obtain, at the output of the R-Ns circuit,

$$f=h_0\,k\,\omega^2 \sin(\omega t+\psi), \tag{14}$$

where ψ is the angle of phase shift of the pulse frequency relative to the G-force.

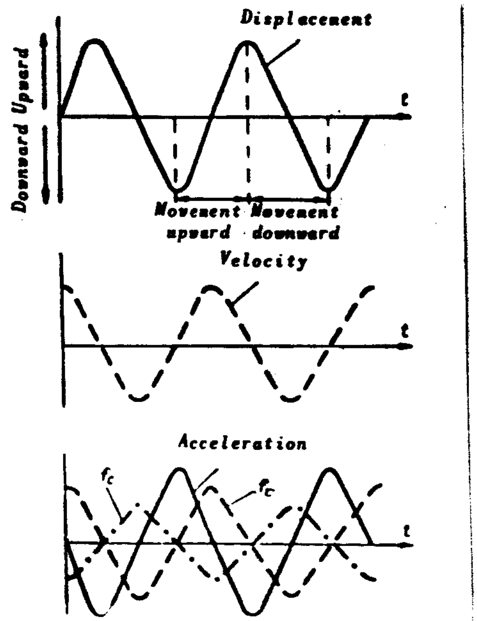

Fig.5 Graphs of Displacement, Velocity, and Acceleration Acting on an Organism and the Pulse Frequency at the Output of Two R-Ns Circuits

Consequently, this receptor-neuron system at a fixed frequency of variation of the mechanical force represents a criterion for the amplitude of these vibrations.

With respect to determining the sign of the acceleration acting on the organism, Fig.5 shows the curves of the displacement of the animal, acceleration, and change of pulse frequency at the output of two R-Ns circuits, with the greatest differences in the characteristics leading to a substantial phase shift of the vibrations ψ.

Thus, if the R-Ns circuit has the same dynamic properties as an electric circuit with a large inductance, then the changes in the pulse frequency f_L /17 in this circuit will show a phase lag relative to the acceleration variations by an angle ψ close to 90° (the pulse frequency in the circuit will increase as the animal moves "upward").

If the dynamic properties of the R-Ns circuit are close to an electric circuit with a large capacitance, the changes in the pulse frequency f_c in the R-Ns system will exhibit a phase lead relative to the acceleration variations by an angle ψ close to 90°. The pulse frequency in the circuit will then increase as the animal moves "downward".

An analysis of these dynamic properties of the R-Ns circuits will permit the following general conclusions:

The receptors of the otolithic portion of the vestibular apparatus perceive accelerations acting on an organism.

In subsequent links of the R-Ns circuit (depending upon its properties) processes of differentiation or integration of acceleration may take place.

The otolithic portion of the vestibular apparatus thus "measures" velocity, acceleration, and the first derivative of acceleration acting on an organism.

BIBLIOGRAPHY

1. Gazenko, O.G., Chekhonadskiy, N.A., Yegorov, B.B., and Razumeyev, A.N.: Vestibular Apparatus and its Elementary Model. Summaries of Reports and Communications at the First All-Union "Man-Machine" Conference (Vestibulyarnyy apparat i yego elementarnaya model'. -Tezisy dokladov i soobshcheniy na I Vsesoyuznoy konferentsii "Chelovek - avtomat"). Moscow, 1963.

2. Gazenko, O.G., Razumeyev, A.N., Yegorov, B.B., and Chekhonadskiy, N.A.: Measurement of the Rhythmics of Neurons of the Reticular Formation on Exposure to Transverse G-Forces (Izmereniye ritmiki neyronov retikulyarnoy formatsii pri poperechnykh peregruzkakh). Dokl. Akad. Nauk SSSR, Vol.155, No.5, 1964.

3. Magnus, R.: Orientation of the Body (Ustanovka tela). Moscow, Izd. Akad. Nauk SSSR, 1962.